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Light attenuation in a 14-year-old loblolly pine stand as influenced by fertilization and irrigation

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Abstract We examined empirical and simulated estimates of canopy light attenuation at SETRES (Southeast Tree Research and Education Site), a 2×2 factorial study of water and nutrients. Fertilized plots had significantly lower under-canopy PAR transmittance (T_c) when compared to non-fertilized plots. Light interception efficiency, as measured by the canopy cosine-corrected light extinction coefficient, G , was significantly lower in irrigated plots for all dates examined. Estimates of G ranged from a low of 0.36 in irrigated plots in September to a high of 0.64 in March for control plots. Study-wide analyses indicate that a G of 0.50 and a k (uncorrected light extinction coefficient) of 0.69 may be reasonable parameter estimates of canopy light extinction in intermediate-aged loblolly pine plantations across a range of stand conditions and seasons when site-specific data are unavailable. Simulated T_c from our version of the BIOMASS model corresponded well to the empirical estimates. Varying the vertical distribution of foliage in simulations (from 10:60:30 to 40:40:10% in the upper, middle, and lower canopy positions, respectively) resulted in only a ±7% change in total PAR intercepted, whereas varying G from 0.3 to 0.7 resulted in a 67% and 31% increase in light intercepted for control and fertilized plots, respectively. Decreased G resulted in an increased proportion of beam radiation intercepted – 63–67% of total PAR intercepted – by the middle canopy where 55–60% of the foliage was found. We hypothesize that proportionally increased productivity observed in irrigated treatments may be attributed to increased beam radiation intercepted deeper into the canopy by a greater foliage area.

Key words LAI · PAR · Light extinction · Pine**Introduction**

Canopy architecture and leaf area index (LAI) determine the amount of incident light intercepted by a forest canopy. Canopy architecture is defined by the vertical and horizontal distribution of canopy foliage and branch biomass. Stand structure and development, along with resource supply, strongly influence canopy architecture and light interception, by determining both the production and distribution of branch and foliage biomass. For loblolly pine (*Pinus taeda* L.), Vose and Allen (1988) demonstrated a linear relationship between nutrient supply and LAI. Increased productivity with fertilization can be attributed to increased LAI and, subsequently, increased PAR intercepted (Dalla-Tea and Jokela 1991); the effect of water supply on LAI remains less clear (Albaugh et al. 1998). Much remains unknown on the influence of both water and nutrition on canopy foliage distribution, light attenuation, and whole-canopy PAR absorption.

The amount and arrangement of foliage and branch biomass of a canopy profile determines the rate of light attenuation through the canopy. The diminishment in quantum flux with increased depth can be modeled as the coefficient of light attenuation, k , as used in the Beer-Lambert equation (Monsi and Sakei 1953). This attenuation coefficient is an index of the efficiency of light capture, or light intercepted per unit LAI (Kira et al. 1969). Estimates of k may be relatively constant among and within species (Jarvis and Leverenz 1983; Pierce and Running 1992; Vose et al. 1995), and they have been found to vary within a species as influenced by canopy architecture (Smith et al. 1992). However, k varies with solar angle (Campbell and Norman 1989; Sinclair and Knoerr 1982). Thus, the cosine corrected light extinction coefficient, G , may be a more consistent estimator of canopy light extinction. Estimates of G are difficult to find in the literature. Sinclair and Knoerr (1982) found a

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G of 0.46 for a 15-year-old loblolly pine plantation. Sampson and Smith (1993) found G to vary from roughly 0.3 to 0.8 for a range of stand and site conditions in lodgepole pine (*P. contorta* var. *latifolia*) stands in Wyoming. Whole canopy light interception therefore depends on the amount and distribution of foliage and branches, as well as the manner in which branches and foliage attenuate light.

Light capture by a forest canopy consists of direct beam, sky diffuse, and scattered diffuse radiation. The relative amount of absorption of each fraction depends primarily on solar altitude, sky conditions, LAI, and canopy architecture. The relative amount of direct beam radiation increases with solar altitude, clear skies, low particulate concentrations, and low humidity. Conversely, the relative amount of sky diffuse radiation increases with particulate concentration and humidity. Canopy architecture ultimately influences the relative interception of each fraction. The relative contribution of these PAR fractions to whole-canopy carbon gain remains unclear. Models can simulate these features, and provide insights to develop hypotheses concerning foliage distribution and light attenuation that may be tested in the field.

We used fertilization and irrigation treatments in a 13-year-old loblolly pine stand to enable us to achieve these objectives: (1) to quantify the effects of irrigation, fertilization, and their interactions on light interception, and (2) to estimate the uncertainty of light extinction and foliage distribution on light interception in these stands by using the BIOMASS model.

Materials and methods

Site and stand description

The study site was located in the Sandhills of Scotland County, North Carolina on an infertile, excessively well drained sandy soil. Annual precipitation averages 1200 mm, with extended drought periods possible during the above-ground growing season. This site was hand planted on a 2x3 m spacing with loblolly pine (*Pinus taeda* L.) in 1985 after felling of the previous natural longleaf pine (*P. palustris* Mill.) stand. In January 1992, sixteen 50x50 m (0.25 ha) treatment plots with a 30x30 m measurement plot centered within each treatment plot were established. Treatments consisted of a 2x2 factorial combination of nutrition and water additions replicated four times. Nutrition treatments began in March 1992, and consisted of optimum nutrition through fertilization or no addition. Optimum nutrition was defined as: (1) maintaining a foliar nitrogen (N) concentration of 1.3%, (2) maintaining foliar macro-nutrient concentration: N concentration ratios of 0.10 for phosphorus (P), 0.35 for potassium (K), 0.12 for calcium (Ca), and 0.06 for magnesium (Mg), and (3) maintaining foliar boron (B) levels greater than 12 ppm. Water treatments, which began in April 1993, were: (1) natural precipitation and (2) natural precipitation plus irrigation applied to meet the target soil water content level. Irrigation events were targeted to maintain soil water content at greater than 3.0 cm soil water content in the surface 50 cm of soil (40% available water content) as determined from volumetric soil water content measured with time domain reflectometry (TDR).

Initial mean tree height, diameter, stand basal area, volume, LAI, and density (1260 stems ha⁻¹) were similar (no statistically significant differences detected) in all plots prior to treatment imposition. Complete control of non-pine vegetation in the treatment plots has been maintained since 1992 through a combination of

mechanical and chemical (glyphosate) methods. The study site description has been fully described elsewhere (Albaugh et al. 1998).

PAR sampling

A preliminary sampling study was conducted to determine the sampling protocol for gathering estimates of under-canopy PAR using a Decagon Light Ceptometer at SETRES. We used two criteria to evaluate the sampling intensity. First, we wanted to sample each plot in a single day within a time window that corresponded to 2 h prior to and following solar noon (highest solar altitude). Second, we wanted a stable estimate of the error and an unbiased estimate of the population mean. The sampling study indicated that 25 point samples, with each sample an average of four separate readings from each cardinal direction (100 per plot) was sufficient to meet these objectives.

We used the Ceptometer to sample under-canopy PAR flux density under clear sky conditions on three dates: March 1996 and 1997 (low LAI) and September 1996 (high LAI). Under-canopy PAR was sampled along equal-distant transects in each plot allowing for a 5 m buffer along the plot edge. Above-canopy PAR (for each minute) was estimated using a quadratic equation fit to hourly PAR data from an on-site meteorological station for each sampling date. These estimates were paired to the individual below-canopy PAR samples to obtain an estimate of canopy PAR transmittance (T_c).

To estimate foliage biomass and, therefore, LAI, 16 trees (four per treatment) were destructively sampled in February 1994 and in January 1996 (Albaugh et al. 1998). Branch diameter, distance from the tree top, and foliage dry weight by age class were measured for all live branches (c.f. Gillespie et al. 1994). Regressions were developed for individual branch foliage biomass based on branch diameter, distance from top, and treatment. Individual branch foliage biomass was summed for each of the 16 trees per sampling period to obtain whole tree foliage biomass. Tree level foliage regressions were then estimated using D^2H as the predictor variable, where D is diameter at breast height and H is live crown length. These equations were applied to the plot mensurational data to obtain a stand level estimates of foliage biomass (see Albaugh et al. 1998). Foliage biomass was multiplied by an average specific leaf area of 32 cm² g⁻¹ (unpublished data), to estimate projected LAI. Leaf area index in September was estimated as the 1996 foliage biomass production plus the 1995 foliage biomass production multiplied by the percent retention of the 1995 foliage in September (Albaugh et al. 1998).

We calculated zenith solar altitude for each under-canopy PAR sample to derive the light extinction coefficients. Solar altitude was estimated in SAS using a series of algorithms (www.crest.org) that were linked to evaluate necessary inputs into the generalized solar altitude equation (Miller 1981). These algorithms include: (1) local solar time (calculated using the local standard time, the equation of time, local standard time meridian, and local longitude), (2) solar declination, and (3) the hour angle (difference between local solar time and solar noon).

We estimated the cosine-corrected light extinction coefficient, G, for each block-plot sample for each of the three collection dates using the cosine-corrected adaptation of the Beer-Lambert equation (Monsi and Saeki 1953) as:

$$G = \frac{\ln(T_c) \cdot \cos \theta}{-LAI} \quad (1)$$

Where: Ln = natural logarithm.

T_c = the ratio of under-canopy to above canopy PAR flux density.

cosine θ = cosine of the zenith solar angle.

LAI = leaf area index estimated from foliage biomass data.

We also estimated study-wide light extinction coefficients, G and k. Individual plot estimates of T_c and a corresponding plot-level estimate of the solar angle and LAI for each sample date were paired, and by using non-linear regression and Eq. 1 we ob-

tained *G*. The uncorrected light extinction coefficient, *k* was estimated in the same manner by omitting solar altitude in Eq. 1. Analyses were performed to look for bias and homogeneity of the regression residuals.

Four sub-plots were established in two control and two fertilized only plots to examine the vertical distribution in the PAR profiles. Four uniformly spaced trees were selected in the treatment plot to insure access with a boom lift. Selected trees had adjacent, intact trees to insure uniformity in the canopy. A 2.5 by 4 m area was demarcated on the forest floor using pin flags to encompass the study trees with the short axis set parallel to the plantation row. We sampled within-canopy PAR, above the marked area, on 19 September 1996 at 1 m intervals throughout the canopy starting at 1 m from the soil surface to the last whole meter before the top of the crown. We obtained 10 estimates of PAR at each height using an average of five point samples per estimate (a total of 50 separate readings per canopy height). A self-propelled boom lift was used to obtain access in the canopy, with a 2 m PVC pipe incremented at 10 cm intervals attached to the front of the lift bucket to help define sample points. The PAR samples were obtained using a Decagon Light Ceptometer.

Foliage profiles were obtained from the 1996 destructively sampled harvest trees (see above) to examine the vertical distribution of foliage in each treatment. Individual branch and foliage weight data were used to develop Weibull distributions for foliage weight for each treatment using Non-linear SAS (SAS 1997). The PDF form of the Weibull (cumulative foliage model) was evaluated as:

$$y = \frac{a * x^{(a-1)} e^{-(x/b)^a}}{b^a} \quad (2)$$

Where: $a = a_0 + a_1F + a_2I + a_3FxI$
 $b = b_0 + b_1F + b_2I + b_3FxI$
 x = relative branch height, and
 Y = cumulative weight (branch or foliage).

Note that *a* is a shape parameter and *b* is the scale parameter that represents the height above which 63% of the mass is found.

We used the branch level data from the 1996 destructive harvest to estimate foliage biomass by 1 m increments, and by canopy third. The foliage biomass estimates were used in the comparison of PAR profile data and to estimate the relative foliage biomass of the canopy for each treatment.

Simulations

Parameterization

We parameterized BIOMASS version 13.0 (Sampson et al. 1997) to examine treatment differences in simulated light interception as

influenced by the vertical distribution of foliage and canopy light extinction (*G*). BIOMASS uses one estimate of *G* and three canopy layers. The proportional amount of foliage in each crown third was obtained from the individual tree foliage profile data as discussed above (Table 1). This analysis assumed that the March profile, or winter dormancy of which one foliage cohort is present in the canopy, approximates the canopy foliage distribution for September. At present we have no reliable data available to estimate the foliage profile when two foliage cohorts are present. Estimates of the temporal change in LAI for control and fertilized only treatments were obtained from monthly LI-COR LAI-2000 plant canopy analyzer (PCA) data collected at SETRES (Albaugh et al. 1998) and the foliage biomass estimates of LAI discussed above. Specifically, the PCA estimates for control and fertilized only plots were normalized to peak LAI to provide the pattern and relative magnitude of LAI display and then multiplied by the biomass LAI estimates for September. The utility of PCA may be in its ability to provide an estimate of the seasonal dynamics of LAI. However, the PCA has been shown to under-estimate LAI for coniferous forest species (Gower and Norman 1991; Smith et al. 1992; Deblonde et al. 1994), with increased under-estimation as LAI increases (Sampson and Allen 1994). However, the PCA may also over-estimate LAI in loblolly pine (Sampson and Allen 1994); on-site data indicates that the PCA under-estimates LAI for this site, although the proportional amount of under-estimation is not constant throughout the year or among treatments. We used an average light extinction coefficient (the mean from the March and September sampling dates) for each treatment (Table 1).

Initial standing biomass in foliage, stems, branches, and fine roots were obtained from Albaugh et al. (1998) (Table 1). This model either inputs daily data for incident shortwave radiation ($MJ m^{-2} day^{-1}$) or estimates it internally. For graphical representation of the output, where necessary, we estimated PAR as 65% of shortwave radiation orbred (Miller 1981). Because this represents a constant fraction of shortwave and, because we focus on normalized data, we use the two interchangeably.

We compared simulated canopy light transmittance with the empirical estimates for control and fertilized only plots. First, we summed the three model outputs of daily intercepted beam, sky diffuse, and scattered diffuse shortwave radiation by canopy third. We then summed, for the year, total shortwave radiation intercepted. The ratio of light interception for each canopy third to total canopy interception provided transmittance for each canopy layer.

Uncertainty analyses were conducted to examine the influence of the vertical distribution of foliage on total canopy light absorption. We varied the relative distribution of foliage among the three canopy layers to examine five foliage profiles: 10:60:30, 20:60:20, 30:50:20, 30:60:10, and 40:40:10% foliage in upper, middle, and lower canopy layers, respectively. We also varied the light extinction coefficient from 0.3 to 0.7 by 0.1 increments to examine their effect on total canopy PAR absorption. Finally, the vertical profile

Table 1 Treatment specific parameters used in the BIOMASS simulations of light interception. These parameters define the stand characteristics and are used at the start of the simulations

Parameter	Parameter description	Units	Control	Fertilized
WFOL	Canopy foliage dry weight	Mg ha ⁻¹	3.00	5.70
WOOO	Stem dry weight	Mg ha ⁻¹	13.00	23.40
WBRA	Branch dry weight	Mg ha ⁻¹	4.90	9.80
WROO	Root dry weight	Mg ha ⁻¹	0.80	0.70
FRACL1	Fraction of foliage in upper canopy layer	unitless	0.394	0.306
FRACL2	Fraction of foliage in middle canopy layer	unitless	0.486	0.540
FRACL3	Fraction of foliage in lower canopy layer	unitless	0.12	0.154
GRNH	Initial average tree height	m	6.16	7.60
TRUNC	Relative height of truncation of ellipses	unitless	0.7397	0.7682
CONCF	Foliage nitrogen concentration	mg g ⁻¹	9.29	11.50
AMX1	Maximum photosynthesis – Summer	μmol m ⁻² proj s ⁻¹	18.15	18.46
AMX2	Maximum photosynthesis – Winter	μmol m ⁻² proj s ⁻¹	4.71	5.18
EXTINC	Canopy light extinction coefficient (<i>G</i>)	unitless	0.495	0.505

of PAR interception for control and fertilized plots was examined with respect to changes in canopy light extinction. Specifically, we examined beam and diffuse light interception by canopy third for three levels of G : 0.3, 0.5, and 0.7.

Statistical analyses

We used SAS (SAS 1987) to examine statistical significance of the main effects of fertilization and irrigation on under-canopy PAR transmittance, LAI, and the light extinction coefficient, G . Individual treatment effects on the vertical distribution in foliage were analyzed using two methods. Cumulative Weibull-distribution parameter estimates were evaluated for significance using mixed procedures [random coefficient and AR(1) errors] in SAS, and the relative distribution of foliage among treatments for crown thirds was examined using ANOVA. An alpha probability level of 0.05 was used in all analyses.

Results

Canopy transmittance (T_C) in the fertilized plots was less than half that of the unfertilized plots for every sampling date. Fertilized plots averaged 21% transmittance in March and 16% transmittance in September while non-fertilized plots averaged 47% in March and 37% in September (Table 2). Transmittance for both fertilized and non-fertilized plots declined between the March 1996 and March 1997 estimates. Estimates of T_C for individual treatments varied from a high of 49% in March of 1996 for control plots to a low of 15% in September of the same year for irrigated-fertilized stands (Table 2). In addition, T_C decreased between March and September 1996 with the addition of the current year foliage cohort, and between March 1996 and March 1997 (except for fertilized only plots).

Irrigation and fertilization affected LAI for all sampling periods, except for September 1996 when no irrigation effect was found (Table 2). Projected LAI ranged from 0.95 in control plots to 2.21 in irrigated-fertilized plots for March 1996. Leaf area index for irrigated-fertil-

ized plots was more than double that of control plots for each sampling date (Table 2).

Within-year differences in T_C for any one treatment reflect seasonal changes in LAI associated with the addition of the current year foliage cohort. However, the relative changes in T_C between the March and September estimates were not proportional to the absolute change in canopy leaf area. Comparing fertilized to non-fertilized plots, non-fertilized plots exhibited a 27% drop in transmittance in September when compared to the March estimates while fertilized plots had a 35% decrease in T_C (Table 2). This was associated with an 82% and 64% increase in LAI for non-fertilized and fertilized plots, respectively (Table 2). However, for non-fertilized plots this represented a 10% increase in light intercepted while fertilized plots intercepted only 5.5% more PAR.

Irrigation influenced the cosine-corrected light extinction coefficient, G , for all collection dates (Table 2). Irrigated plots had 13–16% lower G than non-irrigated plots. For the individual treatments, G varied from a low of 0.36 in September for irrigated only plots to a high of 0.64 in March of 1997 for control plots (Table 2). Within any one sampling period, the greatest variation in G between treatments was ~0.15 (March 1997). Light extinction decreased between the March and September estimates for 1996 with the addition of the current year foliage cohort for all treatments (Table 2). A significant irrigation-fertilization interaction on G was observed in September.

Transmittance declined exponentially with LAI for the study-level analyses of under-canopy PAR (Fig. 1). The study-wide light extinction coefficient, G , was 0.50 ($n=48$; $r^2=0.79$) while the uncorrected light extinction coefficient (k) was estimated as 0.69 ($n=48$; $r^2=0.70$). Slight bias associated with the irrigated only treatments was observed for several dates corresponding to an LAI of approximately 2 and a T_C of 0.4 (Fig. 1).

The within-crown PAR profiles for September 1996 indicated gradual attenuation of light from the top of the canopy to one meter from the soil surface in the control

Table 2 Estimates of under-canopy photosynthetically active radiation (PAR) transmission (T_C), projected leaf area index (LAI), and estimates of cosine-corrected light extinction coefficient, G , derived using the Beer-Lambert equation and estimates of T_C and LAI for three collection dates and four treatments

Parameter	Treatment Means				MSE
	Control	Irrigated	Fertilized	Irrigated and Fertilized	
T_C					
March 1996	0.489	0.446	0.198	0.225	0.06671
Sept. 1996	0.357	0.378	0.165	0.148	0.0600
March 1997	0.425	0.432	0.210	0.188	0.0672
LAI					
March 1996	0.95	1.12	1.82	2.21	0.1916
Sept. 1996	1.67	2.09	3.19	3.42	0.3054
March 1997	1.01	1.32	2.04	2.39	0.2099
G					
March 1996	0.5107	0.4770	0.5686	0.4610	0.0484
Sept. 1996	0.4765	0.3561	0.4408	0.4432	0.0539
March 1997	0.6410	0.4849	0.5871	0.5475	0.0695

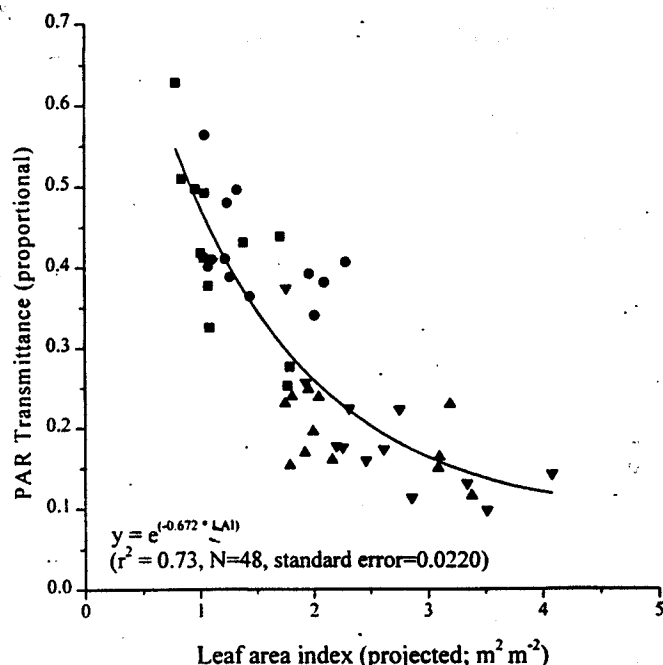


Fig. 1 The relationship between leaf area index and photosynthetically active radiation (PAR) transmittance for three sampling dates and control (squares), irrigated (circles), fertilized (upside down triangles), and irrigated/fertilized (triangles) plots

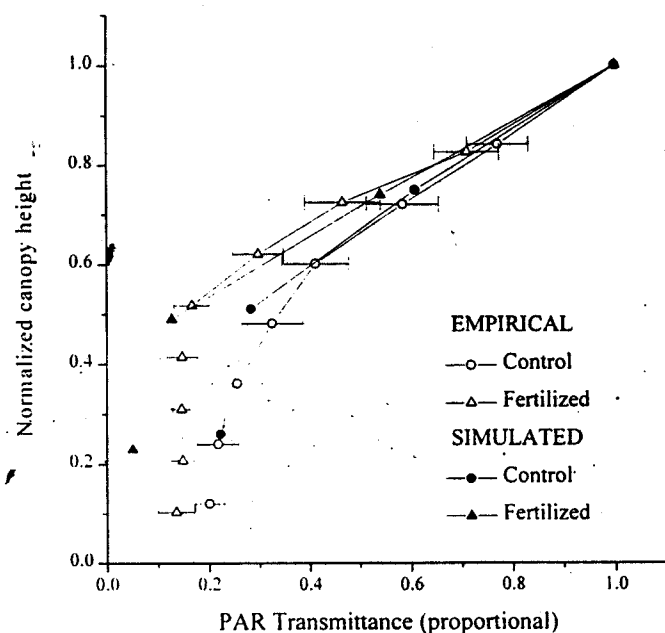


Fig. 2 A comparison of simulated (filled symbols) versus empirical (open symbols) estimates of PAR transmission through the profile of control (circles) and fertilized (triangles) plots. Empirical estimates are from one sampling date in September of 1996 while simulated were calculated using the yearly sum

plots. Fertilized only plots exhibited a marked reduction in PAR with almost all of the available PAR captured through 60% of the canopy (Fig. 2). Fertilized only plots reached a similar transmittance at roughly 50% of the canopy depth as control plots did to the base of the live

Table 3 The alpha (shape) and beta (scale) parameter estimates and statistics for the cumulative Weibull model for four treatments

Parameter	Alpha Estimate	Pr>T	Beta Estimate	Pr>T
Control	2.9243	0.0001	0.4875	0.0001
Irrigated	3.0578	0.3582	0.4819	0.7232
Fertilized	3.1462	0.1282	0.4811	0.6867
Irrigated + fertilized	2.7379	0.2007	0.4636	0.1344

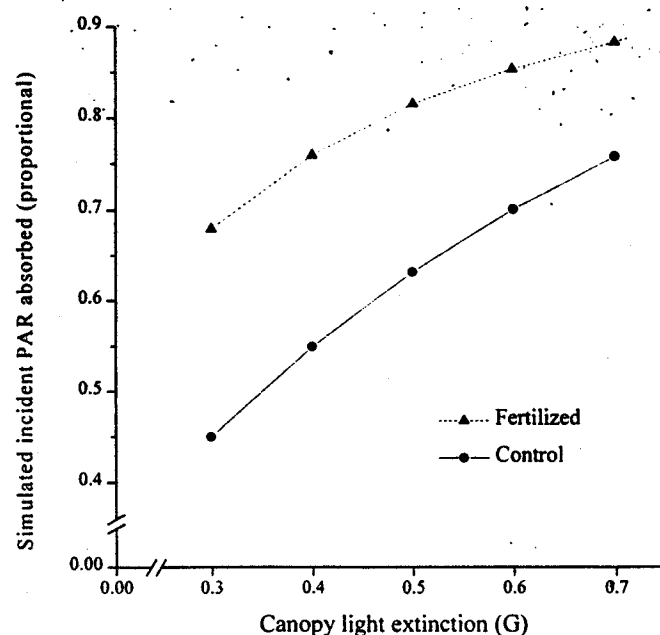


Fig. 3 A comparison of the relationship between four levels of canopy light extinction and proportional simulated incident photosynthetically active radiation (PAR) absorbed for control (circles) and fertilized (triangles) treatments

crown. For each height, fertilized only plots intercepted more PAR than did control plots. Control plots approached, but did not reach, a lower asymptote of canopy PAR transmittance (for these September estimates). Fertilized only plots appear to have reached a lower asymptote in PAR interception fairly high within the canopy. The uniform canopy conditions of the sub-plots used in the analyses of the canopy PAR profiles resulted in lower under-canopy estimates of T_c when compared to the stand-level data; the stands, in general, were less uniform than the subplots (Fig. 2, Table 2).

The treatments did not affect the shape or scale parameters of the Weibull cumulative foliage distribution for the normalized crowns (Table 3). The normalized foliage distributions by crown third indicated that 28–33% of the foliage mass was in the top one-third of the canopy, 54–61% was found in the middle third, and approximately 8–15% of the foliage mass was in the bottom third of the canopy profiles over all treatments. No differences, however, were detected in the tests of significance between treatments among the three canopy classes.

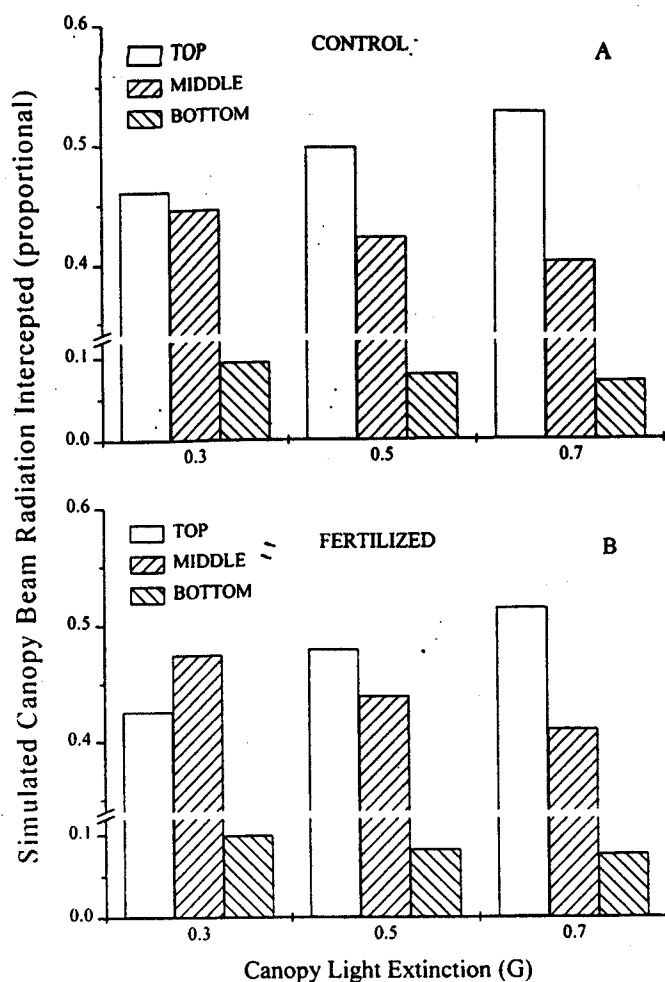


Fig. 4 The proportion of simulated beam radiation intercepted as influenced by canopy light extinction by canopy third for control (a) and fertilized (b) plots

Annual estimates of shortwave attenuation (from simulations) correlated well with the empirical estimates of the PAR profile transmittance for control and fertilized only plots from September (Fig. 2). Simulated transmittance was slightly lower than the empirical estimates in the bottom third of the canopy for fertilized only plots.

Foliage distribution and canopy light extinction exhibited quite different effects on total canopy PAR absorbed. Sensitivity analyses for a range of vertical distributions in foliage indicated only slight differences in total canopy PAR absorbed. The five foliage profiles showed less than 6% of the variation in total absorbed shortwave. In contrast, the canopy light extinction coefficient strongly influenced simulated absorbed radiation (Fig. 3). As expected, the effect was more pronounced for the lower LAI simulations of the control plots which intercepted 45 to 75% of incident shortwave when G ranged from 0.3 to 0.7 (Fig. 3). Fertilized only plots intercepted 68 to nearly 90% of incident radiation for a similar range in G.

Simulations suggested a distinct difference in the manner in which control and fertilized plots intercept in-

cident shortwave radiation. Direct beam radiation represented the greatest proportion of total shortwave intercepted (63–66%). Roughly 46% of beam radiation was intercepted in the first layer for control plots for a G of 0.3 (Fig. 4a). A slightly lower proportion of PAR was intercepted by the second canopy layer. The proportion of total beam intercepted by the first layer increased as G increased. In contrast, fertilized-only plots intercepted 42% of incident beam radiation in the first canopy layer, with proportionally more beam radiation intercepted by the second canopy layer (Fig. 4b). As in control plots, the proportional amount of intercepted beam radiation for the first canopy layer increased as G increased. Intercepted diffuse radiation followed a similar trend with canopy depth as beam radiation. Overall, decreased G resulted in an increased proportion of direct beam radiation intercepted lower in the canopy.

Discussion

Treatment and seasonal differences in under-canopy PAR, and canopy light attenuation, demonstrate the influence of foliage cohort and canopy architecture in determining whole-canopy PAR absorption in this loblolly pine plantation. Decreased canopy light transmittance in the fertilized plots can be explained by the large increase in LAI (Table 2). However, irrigation did not affect T_c even though there was a significant positive effect of irrigation on LAI. We found no treatment influences on the normalized vertical distribution of foliage: undetected differences in the manner in which foliage is displayed (e.g. mean inclination angle, or shoot clumping) in irrigated plots may determine the reduced efficiency of light capture found in irrigated plots. Our findings suggest that whole-canopy PAR absorption depends on the spatial and temporal arrangement and production of foliage as related to their combined effects on canopy light attenuation.

A constant value of G has often been assumed to apply for all stands of a given species, however studies may be found that challenge the validity of this assumption. Sampson and Smith (1993) found that G ranged from 0.28 to 0.70 for lodgepole pine stands in a small region of southeastern Wyoming. Variation in G resulted from differences in canopy architecture among stands; G decreased as LAI increased, as canopy gaps increased, and as mean zenith foliage angle decreased. For loblolly pine in this study, G decreased with fertilization and during the year within each treatment associated with the addition of the current year foliage cohort. Both findings are due to an increase in LAI and, therefore, a decrease in the efficiency of light capture, and are consistent with observations by Smith et al. (1992) and Sampson and Smith (1993). The seasonal influence LAI on canopy light extinction has been observed by Dalla-Tea and Jokela (1991), who reported a lower light extinction coefficient, k, in September for loblolly pine (termination of the current year foliage cohort development). And Gholz et al.

(1991) observed a similar seasonal trend in k , associated with the yearly pattern in LAI for slash pine (*P. elliotii* var. *elliottii*).

Intensively managed plantation loblolly pine and slash pine stands would be expected to have more homogeneous, uniform canopies as compared to natural pine stands. Plantations have a more even distribution of trees, with a generally similar resource supply to each tree due to intensive cultivation at establishment and throughout the life of the stand. As such, differences in G among stands would most likely be associated with phenological changes in LAI rather than differences in canopy architecture as a result of stand structure as observed in lodgepole pine stands, for example (Sampson and Smith 1993; Long and Smith 1990; Smith and Long 1989). These factors would act to minimize the variability in G found.

When data are otherwise unavailable, a G of 0.5 is often assumed, regardless of the species. This greatly simplifies modeling light attenuation; a G of 0.5 corresponds to the assumption of a spherical distribution of foliage (an equal LAI normal to the beam regardless of the solar altitude) in a random, homogeneous canopy (Russell et al. 1989). Our study-wide analyses of G (0.5) was statistically identical to the theoretical calculations. There are, of course, simplifying assumptions when using the Beer-Lambert equation to model light attenuation through discontinuous forest canopies that have often been questioned, but these assumptions may be immaterial if the intent is to model average light condition below the canopy (Larsen and Kershaw 1996). Our results suggest that a G of 0.50 may be used for relatively homogeneous canopies of intermediate-aged plantation loblolly pine stands when stand- and season-specific data are lacking. Simulated light interception was remarkably similar to the one point-in-time estimate from the empirical data (Fig. 2). Over-estimation of T_c in lower canopy positions for the fertilized only plots can be, at least partially, attributed to an over-estimate of G for fertilized plots this time of the year (Table 2). The generally good agreement between empirical and simulated light transmission permits extrapolation to potential mechanisms influencing light attenuation and whole-canopy PAR absorption. Varying the vertical distribution of foliage in the model had little effect on total canopy light capture; this finding was somewhat surprising. All things equal, we expected increased whole-canopy light interception with increased foliage biomass near the top of the canopy (c.f. Turton 1985). A lack of model sensitivity to the foliage profile seems unlikely (Fig. 2, McMurtrie and Wang 1993). It seems, rather, that the canopy responds more to the interaction between the vertical foliage profile, LAI, and their effect on light attenuation in determining whole-canopy PAR absorption (Figs. 2, 3); again, no treatment differences in the normalized foliage distribution were found.

These simulations suggest an inverse coupling between the efficiency of light capture and LAI (Figs. 3, 4). Specifically, a lower light extinction coefficient (associated with higher LAI) permits a greater amount of direct beam

radiation (and, therefore, beam diffuse) to attenuate deeper into the canopy at lower irradiance levels. This may be associated with more efficient whole-canopy PAR absorption; more incident PAR at levels below light saturation can be absorbed. This finding has substantial anecdotal support. Increased direct beam transmission attributed to increased foliage clumping or decreased zenith leaf angle – both decrease G (Sampson and Smith 1993) – permits greater direct beam radiation lower into the canopy (c.f. Dalla-Tea and Jokela 1991; Brown and Parker 1994; Larsen and Kershaw 1996).

These simulations suggest that higher productivity associated with greater LAI (and, therefore, lower canopy light extinction), may be fundamentally associated with the observed relationship between LAI and G . For these loblolly pine stands this was associated with a proportionally higher foliage mass in the middle third of the canopy. In all treatments, we observed decreased G with the addition of the current year foliage cohort. Yet, no fertilization effect on G was observed (the dominant determinant of foliage production in this study). Thus, loblolly pine appears to optimize canopy light interception for a "resource equilibrium" leaf area, and compensates architecturally to increase light capture lower in the canopy with the inclusion of the current year foliage cohort.

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